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Divergence and ranking of taxa across the kingdoms Animalia, Fungi and Plantae

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Abstract

In science, species are grouped and ranked in kingdoms, phyla, classes, orders, families and genera and several other intermediate taxa, in a taxonomic hierarchy. However, the ranking of phyla, classes, orders and families across kingdoms is not linked and there is unlikely to be any correlation between these ranks in animals, fungi or plants. In a few recent studies, divergence times have been used to develop more natural groupings within ranks and it has been suggested that divergence times should be used as a universal criterion in high level ranking. It would therefore be desirable to develop more stable and standardized grouping of taxa in phyla, classes, orders and families across the kingdoms using divergence times. However, is this feasible? The origins of the kingdoms have been well-studied, however a comparison of the earliest divergence of major taxa (phyla, classes, orders, and families) across these kingdoms is lacking. We therefore considered that it would be of interest to look at ranking of groups across three kingdoms, Animalia, Fungi and Plantae. Are the ranking in these kingdoms comparable or has one or more kingdoms been more liberal in splitting taxa at the higher levels (e.g phyla, classes, orders, families)? We used paleobiological information from early diverged groups among the kingdoms Animalia, Fungi and Plantae corresponding to the geological time scale for comparisons. As a general rule, we found that groups of Animalia classified as phyla, classes, orders and families, diverged earlier as compared to those of the kingdoms Fungi and Plantae. This suggests that animal taxonomists have been more liberal when splitting ranks at the phylum, class and order levels, while at the family level the ranking across kingdoms is comparable. The common trend of evolutionary events could therefore be applied for re-ranking of some groups, especially at the generic and perhaps family levels. However, it would appear an impossible task to standardize higher level rankings across the kingdoms, as there would need to be huge, and probably unacceptable changes. Basically, the mycologists and botanists would need to split much more at the phylum, class and order levels, while the zoologists would need to combine many of their phyla, classes and orders. The data however, suggests that fungal and plant taxonomists could be more liberal when considering new families, orders, classes and phyla in the future.

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Introduction

Living organisms comprise seven kingdoms (Ruggiero et al. 2015). The kingdoms Archaea (Archaebacteria) and Bacteria (Eubacteria) are classified in the super kingdom Prokaryota (Ruggiero et al. 2015). The kingdoms Animalia, Chromista, Fungi, Plantae and Protozoa are classified in the super kingdom Eukaryota (Ruggiero et al. 2015). There are two subkingdoms and 34 phyla within the kingdom Animalia and they are taxonomically confused (Ruggiero et al. 2015). The kingdom Fungi has been divided into the phyla Ascomycota and Basidiomycota (subkingdom Dikarya; James et al. 2006), and the phyla Chytridiomycota, Glomeromycota and Zygomycota (Ruggiero et al. 2015) based on morphology and phylogeny. The kingdom Plantae (Archaeplastida) has been ranked in various ways comprising lower and higher plants within the same kingdom (Ruggiero et al. 2015). According to a recent classification, the kingdom Plantae is divided into the subkingdoms Biliphyta and Viridiplantae (Burki 2014, Ruggiero et al. 2015). Table 1 summarizes the number of phyla, classes and orders among the kingdoms Animalia, Fungi and Plantae (Ruggiero et al. 2015). Interestingly there is a higher number of phyla, classes and orders within the kingdom Animalia, as compared to the other two kingdoms. This might suggest that taxonomists studying Animalia have been liberal in ranking at these levels, while the mycologists and botanists have been far more conservative.

Table 1. Current number of the taxa among the kingdoms Animalia, Fungi and Plantae (Ruggiero et al. 2015).

Kingdom	No. of Taxa		
	Phyla	Classes	Orders
Animalia	34	100 (96+4)*	598 (590+8)*
Fungi	5	41 (34+7)*	147
Plantae	8	42	211 (209+2)*

*Total number of taxa (named taxa + taxa without names)

Divergence times, paleobiological studies and ranking of taxa

Molecular dating is rapidly developing into one of the most exciting applications in phylogenetic systematics (Bromham & Penny 2003, Kemp 2005, Taylor & Berbee 2006). Molecular timescales provide insights into the history of organisms and are valuable for predicting evolution in the case of organisms with incomplete, or lack of fossil records (Bromham & Penny 2003). A combination of geological and molecular information, i.e. paleobiology or geobiology, with appropriate selection of methods, with representative fossil data, provide reliable divergence times for organisms (Guicking et al. 2006, Eme et al. 2014, Magallón et al. 2015).

In taxonomy, species are grouped and ranked in kingdoms, phyla, classes, orders, families, genera and several other intermediate taxa. Authors have suggested the use of divergence times as universal criteria for ranking taxa, or to construct a natural grouping of the organisms within ranks (Woese et al. 1990, Avise & Johns 1999, Li et al. 2005, Lücking et al. 2009, Prieto & Wedin 2013, Talavera et al. 2013, Zhao et al. 2016, Hongsanan et al. 2016).

Molecular timescales are widely used in animals, fungi and plants to determine the occurrence of evolutionary events (Wang et al. 1999, Mitchell-Olds & Bergelson 2000, Bromham & Penny 2003, Li et al. 2015). The purpose of the present study is to examine the correlation of divergence times of taxa (phyla, classes, orders and families) across the kingdoms Animalia, Fungi and Plantae. The common geological periods are considered based on the early divergences estimated by using available paleobiological information from previous studies (Zhao et al. 2016, Hongsanan et al. 2016). This is mainly to establish the common early divergence times for the taxonomic groups. The aim of this paper is to establish if there are any common trends in the ranking of phyla, classes, orders, families and genera, across the kingdoms Animalia, Fungi and

Plantae, or whether it is random. This will be of considerable interest when considering standardizing the ranking of taxa across the kingdoms based on divergence times.

***Origin and early divergences of organisms grouped as phyla among the kingdoms Animalia, Fungi and Plantae* (Table 2)**

During the Paleoproterozoic-Mesoproterozoic (2500-1000 Mya), the kingdoms Animalia, Fungi and Plantae shared common characters with rapid subsequent divergences (Walker et al. 2012, Eme et al. 2014). The kingdoms Animalia and Fungi diverged during the Mesoproterozoic (1600-1000 Mya) from the super group 'Opisthokonta' (metazoans, fungi and some heterotrophic Protists; Hedges et al. 2004, Adl et al. 2005, 2012, Cavalier-Smith 2010, 2014, Burki 2014). The divergence of the plant lineages occurred around 1379 Mya during the Mesoproterozoic (1600-1000 Mya) from a common eukaryotic ancestor (Bhattacharya et al. 2009).

The earliest groups within the kingdom Animalia, the sponges, hydroids, jellyfish, anemones, corals and comb jellies (phylum Cnidaria) diverged during the Neoproterozoic era (1000-541 Mya, Müller 2001, Müller et al. 2003, Philippe et al. 2009, Park et al. 2012, Jékely et al. 2015). The arthropods (phylum Arthropoda), horseshoe worms (phylum Phoronida), velvet worms (phylum Onychophora), marine deuterostomes, sea stars, sea urchins, sand dollars, sea cucumbers and sea lilies (phylum Echinodermata) diverged in the latter part of the Neoproterozoic era (635-541Mya, Table 2, Rehm et al. 2011, Sperling et al. 2011, Li 2016).

The paleobiological information suggests that the divergence of the phylum Chytridiomycota occurred before the divergence of terrestrial plants, during the Mesoproterozoic era (1242 Mya, Berbee & Taylor 2001, Padovan et al. 2005, Torruella et al. 2012). The common divergence period for the phyla Ascomycota, Basidiomycota and Glomeromycota occurred mainly in the Neoproterozoic to Early Paleozoic (1000-485Mya), parallel to the divergences of terrestrial animals (Schüßler et al. 2001, Berney & Pawlowski 2006, Lücking et al. 2009, Beimforde et al. 2014; see Table 2).

The early divergences of red algae (phylum Rhodophyta) and freshwater microscopic algae (phylum Glaucophyta) in the kingdom Plantae, occurred during the Mesoproterozoic (1600-1000 Mya, Zimmer et al. 2007, Nozaki et al. 2009). Most of the terrestrial groups, the mosses (phylum Bryophyta), liverworts (phylum Marchanatiophyta) and vascular plants (phylum Tracheophyta) within the kingdom Plantae have diverged during the Early Paleozoic (419-541 Mya, Zimmer et al. 2007, Clarke et al. 2011, Cooper et al. 2012; see Table 2).

The summarized early divergences of taxonomic phyla within the kingdoms Animalia (blue), Fungi (orange) and Plantae (green) are shown in Table 2 and Fig. 1. The selection of taxa given in the Table 2 is based on recent studies combining fossil and biological data, and divergence time selection being from early diverged groups. Priority was given to studies focusing on specific organism groups than general studies. It was assumed; that such studies have estimated reliable divergence times using representative biological data and calibrations. However, estimated divergence times from general studies were also used in some cases due the lack of data.

The animal phyla groups show a common divergence during the Neoproterozoic (1000-541 Mya) in the Precambrian. Peterson et al. (2004) and Qun et al. (2007) suggested that most animalian phyla diverged during the Early Paleozoic (before 540 Mya), while Knoll (2014) suggested that the extensive diversification of the eukaryotes occurred during the Neoproterozoic (1000-541 Mya). Most of the early divergences in the phylum Fungi occurred during the Neoproterozoic to Early Paleozoic (1000-485 Mya), while the earliest divergences were during the Mesoproterozoic (1600-1000 Mya). The Chytridiomycota divergence occurred earlier than the divergences of most other fungal groups. However, the basal relationships of the polyphyletic lower fungi, Chytridiomycota and Zygomycota are still unresolved (Tanabe et al. 2005, Kirk et al. 2008). The early divergences of plant groups occurred during the Mesoproterozoic (1600-1000 Mya) and most plant phyla diverged during the Paleozoic (541-252 Mya). Parfrey et al. (2011) suggested that the divergence of red algae and green algae occurred during the Mesoproterozoic and Neoproterozoic. This may suggest that there are two common trends in plant group

divergences. The overall trend is that the Chytridiomycota (early fungi) and Rhodophyta (early plants) evolved earliest follow by Cnidaria (early animals). This was followed by various phyla of Animalia and Fungi and then Plantae. The animal and fungal phyla are generally older than the plant phyla. This may be problematic, as the animal and fungal evolution relied on the plants and therefore the plant phyla should be older.

Table 2. Synopsis of the early diverged groups classified as phyla among the kingdoms Animalia, Fungi and Plantae from recent studies. The 95% confident intervals are given in brackets.

Phyla	Divergence time estimates (Mya)	Geological era	References
Cnidaria	736 (819-686)	Neoproterozoic	Park et al. 2012
Arthropoda	~600	Neoproterozoic	Rehm et al. 2011
Onychophora	589 (607-573)	Neoproterozoic	Rehm et al. 2011
Echinodermata	545	Neoproterozoic	Li 2016
Chytridiomycota	1241.99 (1406.97-1152.70)	Mesoproterozoic	Padovan et al. 2005
Ascomycota	642 (859-504)	Neoproterozoic-Paleozoic	Beimforde et al. 2014
Glomeromycota	~ 720-600	Neoproterozoic	Lücking et al. 2009
Basidiomycota	521 (766-452)	Neoproterozoic-Paleozoic	Garnica et al. 2016
Rhodophyta	1142 (1309-975)	Mesoproterozoic-Neoproterozoic	Zimmer et al. 2007
Bryophyta	496 (580-412)	Neoproterozoic-Paleozoic	Zimmer et al. 2007
Marchantiophyta	484 (509-452)	Paleozoic	Cooper et al. 2012
Tracheophyta	446 (456-425)	Paleozoic	Clarke et al. 2011

Early divergences of organisms grouped as classes among the kingdoms **(Table 3)**

The divergences of hydra, freshwater jellies (class Hydrozoa), true jellies (class Scyphozoa), flower animals (class Anthozoa) and arachnids (class Arachnida) occurred during the Late Neoproterozoic (850-541 Mya, Park et al. 2012). Most other animalian classes (eg. Melocostraca, Insecta) diverged and diversified during the Paleozoic era (541-252 Mya, Regier et al. 2004, Sanders & Lee 2010).

Among the fungi, the highly diversified and species rich Ascomycota diverged into several classes (e.g. class Dothideomycetes, Orbiliomycetes, Pezizomycetes, Sordariomycetes) mainly during the Paleozoic (541-252 Mya, Kirk et al. 2008, Gueidan et al. 2011, Prieto & Wedin 2013, Beimforde et al. 2014). Among the Basidiomycota, the divergences of the classes might also have taken place during the Paleozoic (see Fig. 1).

The phylum Rhodophyta diverged into early classes Florideophyceae and Bangiophyceae during the Neoproterozoic (1000-541 Mya, Yang et al. 2016). The divergences of several other plant groups known as classes, belongs to non-vascular (classes Haplomitriopsida, Jungermanniopsida, and Marchantiopsida) and vascular (class Cycadopsida) occurred during the Paleozoic (359-299 Mya, see the Table 3 and Fig. 1; Zimmer et al. 2007, Cooper et al. 2012, Condamine et al. 2015, Magallón et al. 2015, Villarreal et al. 2016).

Most animalian groups known as classes diverged during the Neoproterozoic (1000-541 Mya) to Early Paleozoic (541-419 Mya). This agrees with Peterson et al. (2004) with the divergence of animalian phyla and classes being prominent during the Neoproterozoic to Early Paleozoic. The divergences of the fungal and plant groups classified as classes mostly occurred during the Early and Late Paleozoic (541-252 Mya).

Early divergences of organisms grouped as orders among the kingdoms **(Table 4)**

Horseshoe crabs (order Xiphosura), shells (order Terebratulida), crayfish, crabs, lobsters, prawns, shrimps (order Decapoda), stony corals, hard corals (order Scleractinia), beetles and weevils (order Coleoptera) diverged mainly during the Paleozoic (541-252 Mya) towards the Late Paleozoic-Early Mesozoic boundary (around 252 Mya, Rehm et al. 2011, Bracken et al. 2010, Sperling et al. 2011, Park et al. 2012, McKenna et al. 2015; see Table 4 and Fig. 1).

The highly diversified classes of Ascomycota and Basidiomycota comprise mycorrhizal, saprotrophic, parasitic, lichenized and non-lichenized fungi groups (e.g. Sebacinales, Ostropales, Mycocaliciales, Boletales, Pyrenulales) which have diverged during the Mesozoic (252-66 Mya, Prieto & Wedin 2013, Garnica et al. 2016, Riess et al. 2016, Sánchez-Ramírez et al. 2015; see Table 4 and Fig. 1).

Table 3. Synopsis of early diverged groups classified as classes among the kingdoms Animalia, Fungi and Plantae from recent studies. The 95% confident intervals are given in brackets.

Class	Divergence time estimates (Mya)	Geological era	References
Hydrozoa	607 (670-571)	Neoproterozoic	Park et al. 2012
Anthozoa	601 (684-544)	Neoproterozoic	Park et al. 2012
Arachnida	545.2 (631.1-475.9)	Neoproterozoic-Paleozoic	Sanders & Lee 2010
Insecta	389.9 (527.4-266.9)	Paleozoic	Sanders & Lee 2010
Pezizomycetes	458 (583-400)	Neoproterozoic-Paleozoic	Beimforde et al. 2014
Orbiliomycetes	430 (554-353)	Neoproterozoic-Paleozoic	Beimforde et al. 2014
Dothideomycetes	338 (394-284)	Paleozoic	Gueidan et al. 2011
Sordariomycetes	260 (339-207)	Paleozoic-Mesozoic	Beimforde et al. 2014
Florideophyceae	943 (1049-817)	Mesoproterozoic-Neoproterozoic	Yang et al. 2016
Haplomitriopsida	414 (469-352)	Paleozoic	Cooper et al. 2012
Jungermanniopsida	390 (425-353)	Paleozoic	Cooper et al. 2012
Cycadopsida	274.5 (332.4-235)	Paleozoic-Mesozoic	Condamine et al. 2015

The early divergences of plant groups placed in orders (e.g. Ceramiales) occurred during the Late Paleozoic (395-284 Mya, Yang et al. 2016). Liverworts (e.g. order Marchantiales, Metzgeriales, Pelliales) and aquatic flowering plants, trees and shrubs (e.g. order Magnoliales, Nymphaeales, Sphaerocarpales) diverged during the Late Paleozoic to Mesozoic (up to 66 Mya) or Jurassic-Cretaceous (201-66 Mya, Cooper et al. 2012, Villarreal et al. 2016, Massoni 2014, Bell et al. 2005, Magallón et al. 2015; see Table 4 and Fig. 1).

Table 4. Synopsis of early diverged groups classified as orders among the kingdoms Animalia, Fungi and Plantae from recent studies. The 95% confident intervals are given in brackets.

Order	Divergence time estimates (Mya)	Geological era	References
Xiphosura	~473	Paleozoic	Rehm et al. 2011
Terebratulida	449 (518-355)	Paleozoic	Sperling et al. 2011
Decapoda	~418.56	Paleozoic	Bracken et al. 2010
Coleoptera	253 (268-238)	Paleozoic-Mesozoic	McKenna et al. 2015
Scleractinia	243 (286-203)	Paleozoic-Mesozoic	Park et al. 2012
Lingulida	191 (281-128)	Paleozoic-Mesozoic	Sperling et al. 2011
Rodentia	63.97 (76.01-56.64)	Mesozoic-Cenozoic	Písano et al. 2015
Sebacinales	252 (391-166)	Paleozoic-Mesozoic	Garnica et al. 2016
Ostropales	189 (221-155)	Mesozoic	Prieto & Wedin 2013
Mycocaliciales	152 (226-87)	Mesozoic	Prieto & Wedin 2013
Boletales	132.6 (186.2-90.2)	Mesozoic	Sánchez-Ramírez et al. 2015
Pyrenulales	120 (173-66)	Mesozoic	Prieto & Wedin 2013
Ustilaginales	95 (143-58)	Mesozoic-Cenozoic	Riess et al. 2016
Chaetothyriales	72 (110-35)	Mesozoic-Cenozoic	Prieto & Wedin 2013
Ceramiales	335 (395-284)	Paleozoic	Yang et al. 2016
Metzgeriales	285 (322-248)	Paleozoic-Mesozoic	Cooper et al. 2012
Pelliales	278 (337-214)	Paleozoic-Mesozoic	Cooper et al. 2012
Marchantiales	196 (251.9-157.4)	Mesozoic	Villarreal et al. 2016
Sphaerocarpales	169 (234-115)	Mesozoic	Villarreal et al. 2016
Nymphaeales	174.42-134.79	Mesozoic	Bell et al.2005
Magnoliales	164.2-115	Mesozoic	Massoni 2014

In summary, the animals grouped as orders evolved during the Paleozoic-Mesozoic (419-66 Mya), which is earlier than the fungal (Mesozoic, 252-66 Mya) and plant (Jurassic-Cretaceous,

201-66 Mya) orders. The number of order taxa in the kingdom Animalia is higher than the kingdoms Fungi and Plantae (Ruggiero et al. 2015). The expansion into new niches by the early diverged animals might have resulted in a higher evolutionary rate with large numbers of taxa (Peterson et al. 2004).

***Early divergences of organisms grouped as families among the kingdoms* (Table 5)**

The large number of families among the three kingdoms made it difficult to select early diverged groups. However, the representative selected divergence information related to the groups known as families in the kingdom Animalia mostly diverged during the Mesozoic (252-66 Mya, Table 5). In the kingdoms, Fungi and Plantae, the common divergences of taxa grouped as families occurred during the Middle of Mesozoic (Jurassic period) to the Cenozoic (201-2.8 Mya, Table 5).

Magallón et al. (2015) suggested that angiosperm plant families diverged continuously during the Middle of Mesozoic to the Middle of Cenozoic (134-33.9 Mya). They further suggested that an unexpected diversification and species richness occurred within the kingdom Plantae and the reason is unclear (Magallón & Sanderson 2001, Magallón et al. 2015).

Table 5. Synopsis of early diverged groups classified as families among the kingdoms Animalia, Fungi and Plantae from recent studies. The 95% confident intervals are given in brackets.

Family	Divergence time estimates (Mya)	Geological era	References
Astartidae	288.2 (307.3-269.2)	Paleozoic	Gonzalez & Giribet 2015
Glypheidae	248-242	Mesozoic	Bracken-Grissom et al. 2014
Crassatellidae	224.0 (320.2-140.6)	Paleozoic-Mesozoic	Gonzalez & Giribet 2015
Palinuridae	221-210	Mesozoic	Bracken-Grissom et al. 2014
Machaerotidae	206.57 (215.96-197.3)	Mesozoic	Cryan & Svenson 2010
Parastacidae	183 (185-177)	Mesozoic	Toon et al. 2010
Cynipidae	54	Cenozoic	Buffington et al. 2012
Elapidae	31.2 (35.6-26.9)	Cenozoic	Kelly et al. 2009
Otariidae	3.85-1.68	Cenozoic	Fulton & Strobeck 2010
Annulatascaceae	300-200	Paleozoic-Mesozoic	Vijaykrishna et al. 2006
Parmeliaceae	112 (135.47-92.97)	Mesozoic	Divakar et al. 2015
Coccotremataceae	111 (156-70)	Mesozoic	Prieto & Wedin 2013
Icmadophilaceae	90 (135-50)	Mesozoic-Cenozoic	Prieto & Wedin 2013
Serpulaceae	64 (80-58)	Mesozoic-Cenozoic	Skrede et al. 2011
Ochrolechiaceae	59 (99-25)	Mesozoic-Cenozoic	Prieto & Wedin 2013
Diplocystidiaceae	38.22 (57.15-21.76)	Cenozoic	Wilson et al. 2012
Bolletinellaceae	36 (54.48-18.7)	Cenozoic	Wilson et al. 2012
Arctomiaceae	9 (16-3)	Cenozoic	Prieto & Wedin 2013
Marchantiaceae	123.5 (173.9-77.8)	Mesozoic	Villarreal et al. 2016
Araceae	121.7	Mesozoic	Nauheimer et al. 2012
Aytoniaceae	111.3 (152.5-80.2)	Mesozoic	Villarreal et al. 2016
Aristolochiaceae	147.3-103.2	Mesozoic	Massoni 2014
Lauraceae	147.2-92.2	Mesozoic	Massoni 2014
Annonaceae	98-89	Mesozoic	Pirie & Doyle 2012
Geraniaceae	48 (57-39)	Cenozoic	Sytsma et al. 2014
Vivianiaceae	35 (44-28)	Cenozoic	Sytsma et al. 2014
Melianthaceae	14.4 (20-10)	Cenozoic	Sytsma et al. 2014

Is ranking based on divergence times possible across the kingdoms?

In the present study, we compare ranking of phyla, classes, orders and families across the kingdoms Animalia, Fungi and Plantae based on divergence times. In general, the animal groups classified as classes, orders and families have diverged before similar taxonomic groups in the kingdoms Fungi and Plantae. There are common divergence periods for similar taxa among the kingdoms Fungi and Animalia. Mora et al. (2011) estimated species diversity as ~7.77, 0.611 and 0.298 million species within the kingdoms Animalia, Fungi and Plantae respectively.

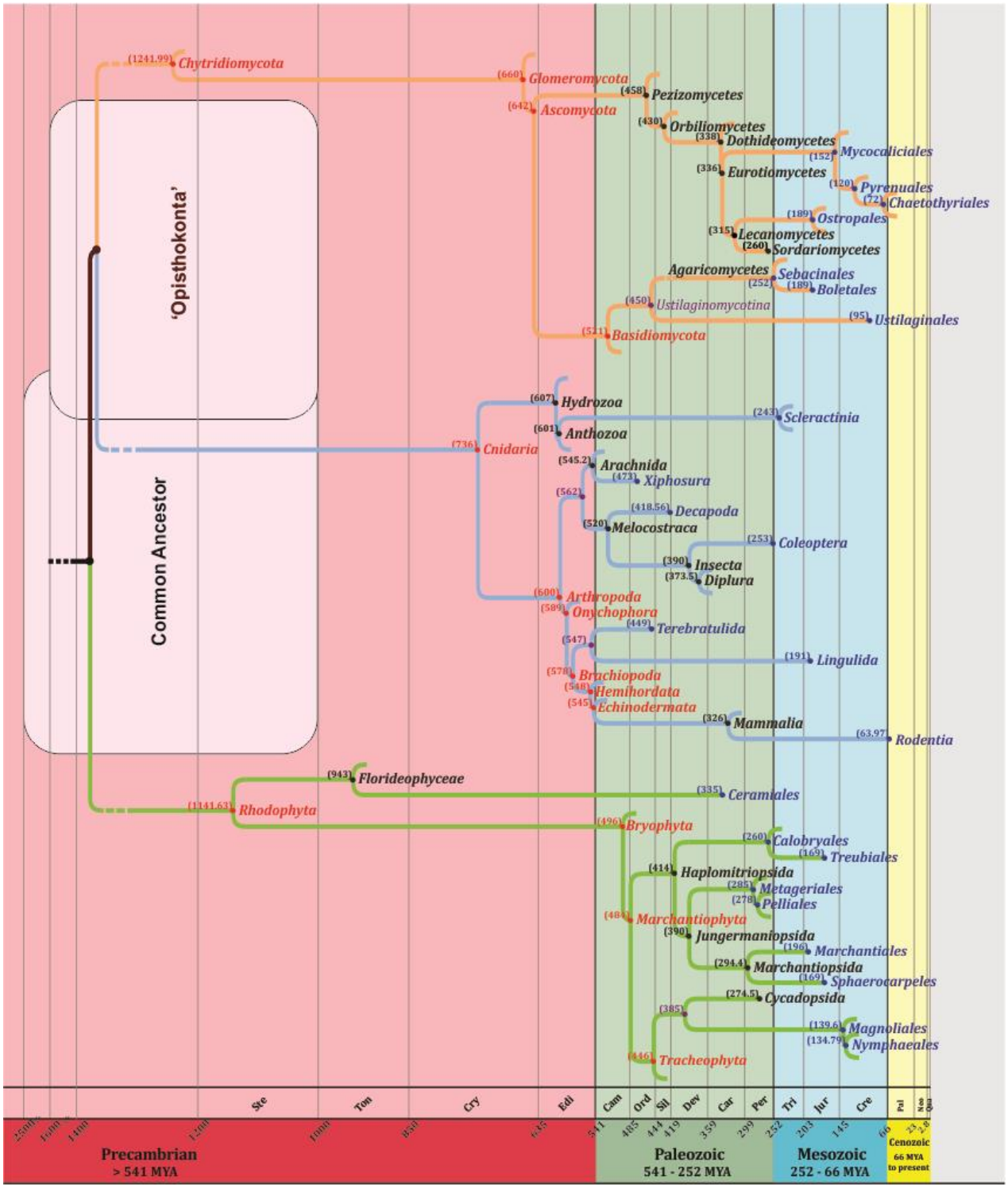

Fig. 1 – Earliest divergence times for phyla, classes and orders among the kingdoms Animalia, Fungi and Plantae. Ste-Stenian, Ton-Tonian, Cry-Cryogenian, Edi-Ediacaran, Cam-Cambrian, Ord-Ordovician, Sil-Silurian, Dev-Devonian, Car-Carboniferous, Per-Permian, Tri-Triassic, Jur-Jurassic, Cre-Cretaceous, Pal-Paleogene, Neo-Neogene, Qua-Quaternary (Walker et al. 2012). Colour bars – kingdom Animalia (blue), Fungi (orange), Plantae (green). The figure is based on divergence times, not on the ancestral relationships. The colour of the letters and dots indicate the taxa, as phylum (red), class (black), order (blue), other intermediate taxa (purple). Mean divergence times are given within brackets as Mya. The divergences of the three kingdoms from common ancestors are based on Bhattacharya et al. (2009).

Here we suggest a hypothesis that needs further consideration. Since the divergence times of the animal groups are generally older than most plant and fungi groups, it is likely that animal taxonomists have been more liberal in introducing higher taxa than plant and fungal taxonomists.

Plant and fungal taxonomists may therefore be able to be less conservative when it comes to introducing new higher level taxa, such as classes and orders. Certainly, in the case of the fungi, were we rely on a limited number of phenotypic characters, we should start to incorporate evolutionary events to increase the resolution of our phylogenies and thus ranking of genera, families, orders, classes and phyla. Evolutionary events could be applied for future ranking of living things and it may be possible to develop a stable and natural classification system for all organisms. This however would not only be a formidable and may be an impossible task, but it may also be unnecessary to establish groupings based on evolutionary events, as a practical ranking based on phylogenies and morphology may be more desirable to the various groups of scientists.

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